

A NATURAL INTERGENERIC HYBRID IN THE $x = 6$ GROUP OF THE ASTEREAE (ASTERACEAE)

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ABSTRACT

A single plant found west of Zacatepec, Puebla, Mexico, is recognized as a hybrid between members of two $x = 6$ genera of Astereae based on intermediacy of characters and reduced fertility. The plant is regarded as *Xanthocephalum humile* (Kunth) Benth. \times *Isocoma* (*Haplopappus*) *veneta* (Kunth) E. Greene. The existence of this and two other natural hybrids of similar origin supports the hypothesis that the genera of Astereae having $x = 6$ are more closely related to one another than any is to genera having other base chromosome numbers, but should not be interpreted as evidence for uniting the genera.

KEY WORDS: Asteraceae, Astereae, *Haplopappus*, *Isocoma*, *Xanthocephalum*, hybrid, Mexico.

RESUMEN

Una planta encontrada al oeste de Zacatepec, Puebla, México ha sido reconocida como un híbrido entre dos $x = 6$ géneros de Astereae basado en fertilidad reducida y caracteres intermedios. La planta es considerada *Xanthocephalum humile* (Kunth) Benth. \times *Isocoma* (*Haplopappus*) *veneta* (Kunth) E. Greene. La existencia de éste y otros dos híbridos de origen natural sostiene la hipótesis de que los géneros de Astereae que tienen $x = 6$ están más cercanamente relacionados unos a otros que cualquiera de éstos con otros géneros con diferentes números cromosómicos base, no obstante esto no debe ser interpretado como evidencia para unir los géneros.

Found west of Zacatepec, Puebla, Mexico was a single plant, *Hartman & Funk* 4127, 19 Aug 1976 (RM and TEX), which has the following combination of features unlike that of any plant previously known to science:

Sprawling perennial herb; stems longitudinally ridged, 15–25 cm long, reddish-brown to purple, densely villous, less so with age, the internodes 2–12 mm long. *Leaves* alternate, often with fascicles of secondary leaves in axils, lanceolate to linear-lanceolate or occasionally linear, 15–30 mm long, 1–5 mm wide, the apex mucronate, the base gradu-

ally tapered, the margins with 1–3 (–4) salient, mucronate teeth per side, often not paired, the adaxial surface sparsely to moderately villous, pitted on drying, the veins obscure, less so on the slightly paler abaxial surface. **Capitulescence** a terminal, corymbose cluster of 4–8 heads; peduncles 5–30 mm long, bracteate, the bracts linear to scale-like, densely villous, sparsely so with age. **Heads** radiate, 7–8 mm high and 14–18 mm wide in flower, 7–9.5 mm high in fruit (pressed material); involucre hemispheric, 5–6 mm high, 7–9.5 mm wide, the phyllaries in 3–4 (–5) series, imbricate, oblong to narrowly oblanceolate, appressed, 1–5 mm long, the lower portion thickened, stramineous, the upper 1/2–1/4 herbaceous, the apex mucronate; receptacles flat to slightly convex, alveolate, the alveolae rimmed by scales 0.2–0.5 mm long. **Ray florets** hermaphroditic (Fig. 1A), 12–15; corolla yellow, the tube 1.7–2 mm long, 0.3–0.4 mm in diameter, moderately to densely villous (Fig. 1A), the lamina broadly oblong to elliptic, 5–6.5 mm long, 1.8–2.2 mm wide, with 4 nerves, the lobes irregular, 0.1–0.5 mm long; anthers 3–4, not well developed; style branches 1.3–1.5 mm long, either linear and appearing strigmate throughout or with deltate appendages; achene oblong to obovoid, 1.9–2.2 mm long, tan, antrorsely pubescent; pappus bristles somewhat unequal, 1.5–2.5 mm long, tan. **Disk florets** hermaphroditic, 32–40; corolla yellow, goblet-shaped, the tube 2.5–2.7 mm long, 0.3–0.4 mm in diameter, sparsely villous, the throat 1.2–1.5 mm long, 0.8–0.9 mm in diameter, glabrous, the lobes narrowly triangular, 0.5–0.7 mm long, glabrous; anthers 5, functional; style branches 1–1.2 mm long with deltate appendages; achene obovoid, 2.8–3 mm long, tan, antrorsely pubescent; pappus bristles unequal, 2–4 mm long, tan. Mexico: Puebla: salt flat (elev. ca. 2300 m), ca. 4.8 km WNW of Zacatepec on hwy 136. With *Xanthocephalum humile*, scattered individuals of *Isocoma veneta*, and species of *Erigeron*, *Suaeda*, *Atriplex*, *Bontelonia*, and *Distichlis* in the immediate vicinity.

There are two possible explanations for the differences between this plant and known species: either it is a new species, or it is a hybrid between related but distinct taxa. Based on the data given below, we believe the latter to be the case.

The plant was found with *Xanthocephalum humile* (Kunth) Benth. and *Isocoma veneta* (Kunth) E. Greene [= *Haplopappus venetus* (Kunth) S. E. Blake], two species of a group of genera of the Asteraceae that several authors have considered to be related. The bases for this assessment are the common base chromosome number of $x = 6$ and shared morphological characters including goblet-shaped disk corollas (first noted by Jackson 1966), deltate style-branch appendages on the disk florets, and rectangular epidermal cells on the adaxial surface of the ray corolla, as shown in Figure 1C (Hartman 1990; Hartman et al. 1987; Lane 1980, 1982; Lane & Hartman 1984, 1985; Lane et al. 1987) among other features (De Jong & Beaman 1963; Keil & Stuessy 1977). In addition, many members of the group grow in saline or alkaline habitats (Robinson 1893; Steyermark 1937; Turner 1972; Mayes 1976; Watson 1977; Lane 1983). Further, Jackson (1966), Jackson & Dimas (1981), and Venugopalan (1966) have reported experimental hybrids between some of the species belonging to this group

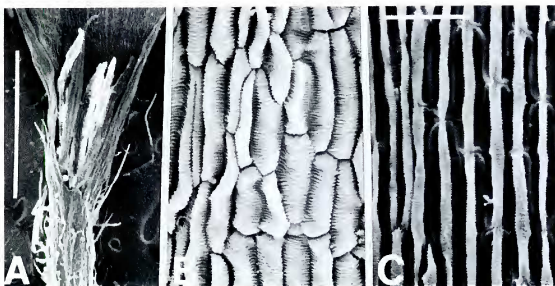


FIG. 1. Scanning electron micrographs of ray florets (scale for A = 1 mm, scale for B and C = 50 μ m). A. Tube and lower portion of lamina of a ray floret from *Hartman & Funk 4127* (RM) showing the poorly developed anthers (light colored) in proximity to two rudimentary adaxial lobes (dark colored) and the villose tube. B. Adaxial epidermis of the lamina of a floret shown in Fig. 1A. C. Adaxial epidermis of the lamina of a ray floret of *Xanthocephalum humile* (Lane 2395, TEX), showing an epidermal pattern typical of all members of the $\pi = 6$ genera of *Astereae*. Specimens were prepared and photographed as described by Lane (1982).

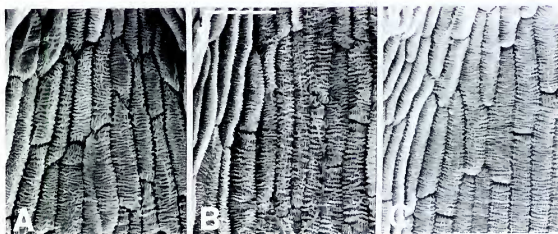


FIG. 2. Scanning electron micrographs of adaxial surfaces of lobes of disk corollas (scale = 50 μ m for all). A. *Xanthocephalum humile* (Lane 2395, TEX). B. *Hartman & Funk 4127* (RM). C. *Isocoma veneta* (Hartman 3830, TEX). Specimens were prepared and photographed as described by Lane (1982). The epidermal pattern shown is typical of all members of the $\pi = 6$ genera of *Astereae*.

of genera; Lane (1980, 1983) found two natural interspecific hybrids in *Xanthocephalum*.

Hartman & Funk 4127 shares a number of features with both of the parental species proposed here. The epidermal cells of the adaxial surface of the disk corolla lobes are identical to those of both *X. humile* and *I. veneta* (Figs. 2A-C), the disk corollas are goblet-shaped, the disk style-branch appendages are deltate, and the plant was found in a saline habitat. However, while the pollen stainability of both species is 98% or greater (Jackson & Dimas 1981; Lane 1980; see Table 1), that of the putative hybrid is only 51.4% (205 of 399 observed grains were stained in lactophenol cotton-blue). Further, only 11 of 19 (57.9%) expanded achenes contained embryos. These indications of reduction in fertility are similar to those found in the natural and artificial hybrids mentioned above (Jackson 1966; Jackson & Dimas 1981; Lane 1980, 1983).

As indicated in Table 1, *Hartman & Funk 4127* has young stems, peduncles, capitula, involucre, and phyllaries like those of *X. humile*, but capitulescence, receptacles, achenes, and pappus similar to *I. veneta*. In all the other features listed in Table 1 and shown in Figure 3, the specimen is intermediate between the two taxa (e.g., habit, leaves, floret numbers, features of the style branch appendages, and achene lengths).

The most striking features of this plant are found in the "ray" florets (Fig. 1A), which have densely villous tubes, unusually deep sinuses, and adaxial epidermal cells (Fig. 1B) quite unlike those of *X. humile* (*I. veneta* is eradiate) shown in Figure 1C. These florets, unlike the ray florets of "good" taxa of the *Astereae*, contain stamens (although rudimentary) and the style-branch appendages in some of the florets resemble more closely those of disk florets. The same phenomena occur in another natural radiate-eradiate hybrid between *Machaeranthera restiformis* B. Turner and *M. gypsophila* B. Turner (Turner & Sanderson 1971; Turner 1973). These anomalous "ray florets" appear to be highly modified disk florets (pers. obs. of the authors). Jackson & Dimas (1981), who experimentally hybridized *I. veneta* with *Haplopappus aureus* A. Gray (a radiate species with $n = 6$), found that the presence or absence of ray florets is a single-gene character (see also Gottlieb 1984), although length of the lamina when ray florets are present is apparently quantitatively inherited. Our observations suggest that length as well as other features of the lamina are polygenically controlled and that some genes involved in disk floret structure can be "turned on" by the allele for presence of ray florets. These hypotheses await testing.

Recently, Guy Nesom brought to our attention two additional putative hybrids. The first (*G. Castillo C. & M. Vazquez 3063*, TEX) was collected in the same area (Mexico: Puebla: road from Zacatepec to El Carmen at

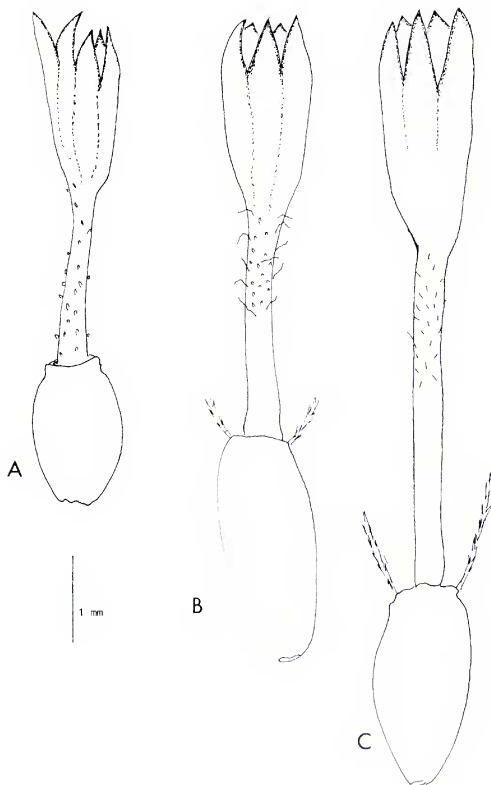


FIG. 3. Line drawings of disk florets, showing goblet-shaped corollas (scale bar as indicated). A. *Xanthocephalum humile* (Lane 2395, TEX). B. Hartman & Funk 4127 (RM). C. *Isocoma veneta* (Hartman 3830, TEX). Achene pubescence of Hartman & Funk 4127 and *Isocoma veneta* is not shown, and only a few of the pappus bristles are depicted.

border with Tlaxcala, 12 Jan 1984). It agrees in general with the description of *Hartman & Funk* 4127 in most morphological features except the leaves are smaller, 10–20 mm long. Interestingly, the ray corollas exhibit one of the following conditions with respect to the adaxial petals: both are suppressed as in a normal floret, one or both is present but reduced in size, both are united into a narrow lamina $1/2 - 4/5$ as long as the abaxial one, or one or both is present as a lateral lobe of the abaxial lamina. The second (*H.H. Iltis, A. Jose, & A. Lasseigne* 802; TEX) was collected approximately 140 km WNW of the site for *Hartman & Funk* 4127 (Mexico: Mexico: on

TABLE 1. Comparison of *Nanthocephalum humile* (data from Lane 1980, 1983), *Hartman & Funk* 4127 (data from the specimen), and *Isocoma veneta* (data compiled from Hall 1928 pp. 223–224, Jackson & Dimas 1981, and personal observation of *Hartman* 3830).

	<i>Nanthocephalum humile</i>	<i>Hartman & Funk</i> 4127	<i>Isocoma veneta</i>
HABIT	prostrate, perennial herb	spreading, perennial herb	shrub
YOUNG STEMS	reddish to purple, villous	reddish to purple, villous	green, glabrous to puberulent
LEAVES	linear to narrowly obovate-spatulate	lanceolate to linear-lanceolate	oblanccolate to spatulate-oblong
MARGIN	usually entire	1–3 salient teeth/side	2–5 salient teeth/side
CAPITULA	solitary	4–8, pedunculate, in corymbose clusters	4–8, \pm sessile, in corymbose clusters
PEDUNCLES	villous, bracteate	villous, bracteate	pubescent but not villous, bracteate
INVOLUCRES	hemispheric	hemispheric	broadly turbinate
HEIGHT	4.3–6.4 mm	5–6 mm	5–8 mm
WIDTH	5.7–6.9 mm	7–9.5 mm	4–6 mm
PHYLLARIES	not resinous	not resinous	resinous
RECEPTACLES	reticulate, scales none	alveolate, alveolae rimmed by scales	alveolate, alveolae rimmed by scales
RAY FLORETS	14–32, pistillate	12–15, hermaphroditic (anthers rudimentary)	0
COROLLA TUBES	trichomes glandular and uniseriate	densely villous	—
DISK FLORETS	29–46 (80)	32–40	15–25 (30)
COROLLA LENGTH	2.9–4.6 mm	4–5.7 mm	5–7 mm
COROLLA TUBES	trichomes glandular	trichomes glandular and uniseriate	glabrous or trichomes sparse, uniseriate
STYL-BRANCH APPENDAGES	papillae elongate, attenuate	papillae elongate, rounded	papillae short, rounded
ACHENES	glabrous, golden brown	sparsely silky-villous, tan	densely silky-villous, light tan
LENGTH	1–2.4 mm	1.9–3 mm	1.8–4 mm
PAPPUS	none or low scaly crown	bristles	bristles
LENGTH	0	1.5–4 mm	3–6 mm
POLLIN STAINABILITY	99.2%	51.4%	98%

former bed of Lago Texcoco at kilometer post 7, WSW of Texcoco, 10 Jan 1978). It fits closely the description of *Hartman & Funk* 4127 except the plant is older and most of the pubescence has been lost and the ray corolla is shorter (tube 2.5–3 mm long; lamina 2.7–3 mm long) and either has a narrow, adaxial lamina nearly equalling the abaxial one or is normal in this respect. Both of these putative hybrids were found to have developed embryos in only 10% of the expanded achenes (1 of 10; limited number available). Pollen stainability was also much lower in these specimens than in *Hartman & Funk* 3027; *Castillo and Vasquez* 3063 had 28.1% stainable pollen (307 of 1090 grains observed), and *Illis et al.* 802 only 13.9% (145 of 1042 grains observed).

Jackson's (1966) hypothesis that taxa of Astereae having goblet-shaped disk corollas are related has certainly been supported by his and others' more recent work, including the present paper. However, if *Haplopappus phyllocephalus* DC., *H. annuus* (Rydb.) Cory, and *H. aureus* (the "phyllocephalus group" of Hartman 1976, 1990) were to be placed in *Isocoma* (*Haplopappus* sect. *Isocoma* sensu Hall 1928) based on the hybrids reported by Jackson & Dimas (1981), then *Xanthocephalum* sensu Lane (1983) should also be accrued, based on the *Xanthocephalum humile* X *Isocoma* (*Haplopappus*) *veneta* hybrid reported here. There are strong morphological and chloroplast DNA restriction site data (D. Morgan, Y. Suh, B. Simpson, M. Lane, unpubl. data) that suggest that the monotypic *Stephanandoria* (Robinson 1892) is very closely allied with *Isocoma* and *Xanthocephalum*. Further, *Xanthocephalum* is clearly related to *Grindelia* (including *Prionopsis*, Morgan, Suh, Simpson, Lane, unpubl. data) to which *Olivaea* (De Jong & Beaman 1963) is also allied (Lane 1982).

Although the experimental and natural hybrids and other data discussed here certainly do indicate relationship of these taxa, we believe that the "lumping" of the several genera, before the detailed morphological and DNA-systematic investigations currently underway (Nesom et al. 1990; Lane, unpubl. data; Y. Suh and B. Simpson, pers. comm.) are completed, would result in a very large genus that would be not only systematically uninformative but also a nomenclatural nightmare. If all were joined to Hall's (1928) *Haplopappus* (in which case the generic name would be *Xanthocephalum* based on priority) as has been suggested by some workers, then it would follow that yet other genera of Astereae should also be united with it. Ultimately, the collapse of most if not all of the tribe into one or a very few genera would result. Such a situation would obscure rather than clarify the phylogeny of the Astereae; for this reason we continue to recognize distinct genera, even though their members may occasionally hybridize.

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